THE INTERPRETATION OF THE RADIAL FIELD OF THE WING IN THE NEMATOCEROUS DIPTERA, WITH SPECIAL REFERENCE TO THE TIPULIDAE.

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(*Communicated by Dr. E. W. Ferguson.*)

(Ninety-two text-figures.)
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Contents.

HISTORICAL.

The study of the venation of the Diptera during the past century has brought about many successive and progressive modifications. The early interpretations of Schiner (1862, pl. 2), Loew (1862) and Osten Sacken (1869) were materially improved by Williston (1908, pp. 37-43) and other subsequent workers. The proposal of the Comstock-Needham system of nomenclature and its application to the order (1899) furnished the most important means for a true knowledge and appreciation of the homologies of the veins. Still more recent work by Tillyard (1919) has served to strengthen our interpretation of the medial and cubital fields of the wing.

In the course of his studies on the Tipulidae, the present writer has long felt dissatisfied with the hitherto adopted interpretation of the radial field of the wing in Diptera (Needham, 1908; Comstock, 1918, 1924; Tillyard, 1919; MacGillivray, 1923). At first sight this interpretation would suggest a double dichotomy of the branches of the radial sector, as in the hypothetical type of insects, and this is indeed true in the two most generalized families of living Diptera (Tanyderidae and Psychodidae). In all higher Diptera, however, one or more branches of this dichotomy have been lost and this has been interpreted as having been brought about by a fusion to the margin of either the upper fork (Ptychopteridae;

Brachycera) or the lower fork (Nematocera) of the primitive dichotomous sector. It has long seemed very strange that in the Diptera we should start with two extremely primitive families (Tanyderidae and Psychodidae) that have no indication of a radial crossvein and then suddenly gain such a vein in the Tipulidae and a few more or less closely allied groups, following which the structure has been completely lost throughout the order. In the present paper, the writer has attempted to demonstrate that the true radial crossvein (r of Comstock (1918, 1924), Needham (1908); ir_1 of Tillyard) has never been developed as a *transverse* element in the Diptera, as shown by all of the above students, and should be omitted as such from any archetype of the order (Tillyard, 1919, fig. 69). The vein lies as a *longitudinal* element in a serial alignment, distinct as a separate unit only in the subfamilies Architipulinae, Tipulinae and Cylindrotominae, and two tribes of the Limoniinae, the Lechriini and some Limoniini. In two earlier papers, the writer had briefly outlined these various interpretations in the subfamily Cylindrotominae (1919, p. 863) and in the Limoniine tribe Pediciini (1918).

Edwards (1926, p. 126) felt inclined to doubt the possibility of two radically different types of radius having been developed within the family Tipulidae. It was for the purpose of attempting to decide this question, which has long been a disputed point in the consideration of the group, that the present writer began a critical comparative survey of the various genera and species, more than 98% of the genera and subgenera, and over 3,000 species of Tipulidae having been available for the purpose. It was soon apparent that two distinct groups were involved, one, represented by the Tipulinae, Cylindrotominae, and the tribes Lechriini and Limoniini, having r present as a *longitudinal* element and forming part of a serial radial vein and with R_4 and R_5 fused to the wing margin; and, secondly, the remaining tribes of the Limoniinae (Pediciini, Hexatomini, Eriopterini, and the aberrant Styringomyini) in which no radial crossvein had been developed, where R_2 had swung cephalad and fused backward from the wing-margin with R_1, where R_4 had been taken from the primitive dichotomous posterior fork of the sector and become more intimately connected with the anterior branch, R_{2+3}, leaving the posterior branch of the radial field to consist of R_5 alone. This rather involved and somewhat mystifying condition of affairs is discussed in some detail in the present paper. A special effort has been made to choose representatives of Australian genera where these showed the points involved. After this critical review of the known Tipulidae, the writer cannot feel but that the main principles as given at this time are correct.

THE PRIMITIVE CONDITION OF THE RADIAL FIELD IN THE DIPTERA.

The condition of the radial field in the two recent families Tanyderidae and Psychodidae is so like that of the archetype of the Diptera that we must consider them as representing the two most generalized living groups. This contention is beautifully upheld by the recent critical work on the body morphology and phylogeny of the group by Crampton (1924-1926) and Edwards (1926). There can be no doubt but that the two families are closely allied, a view that was apparently first suggested by Lameere (1906). In these two groups there are five branches of radius attaining the wing-margin and no indication of a radial crossvein. It should be noted, however, that in the three families of Diptera most closely allied (Ptychopteridae, Trichoceridae and Tipulidae) the number of branches of the sector has already undergone a reduction and in representatives of all of them the *so-called* radial crossvein (r of previous workers) is found.

In the phylogeny of the Diptera (Crampton, 1924-1926; Edwards, 1926) it is now believed that the Ptychopteridae are closely allied to the Tanyderidae and that they either ended as a blind stem, or, possibly, gave rise to certain groups of the Nematocerous Diptera, and through them, the Brachycera. The Trichoceridae appear to lead directly toward the Anisopodidae, from whence the other groups of the Nematocera seem to have been derived. Since, therefore, the only groups of Diptera that are more primitive than these three are the Tanyderidae and Psychodidae, it follows that whatever interpretation is accepted for the Ptychopteridae, Trichoceridae and Tipulidae must be accepted also for all higher Diptera. It is for this reason that the correctness or incorrectness of the accompanying data and interpretations assumes an importance very much greater than would be the case if merely the single family Tipulidae were involved.

THE TWO TENDENCIES OF SPECIALIZATION IN THE RADIAL FIELD IN THE TIPULIDAE.

As was briefly indicated in the historical introduction of this paper, there appear to have been two very distinct tendencies in the Tipulidae that are so profound that both are shown by the oldest known Tipulidae and related groups (Upper Liassic).

These two lines of specialization are as follows:

A. In the subfamily Limoniinae, the three tribes Pediciini, Hexatomini and Eriopterini (together with the aberrant tribe Styringomyini, which apparently must be considered with the Eriopterini in any discussion of the groups) have evidently been derived through some primitive Pediciine ancestor from a type that was not unlike our recent Tanyderidae. The upper branch of the anterior fork of the primitive sector has swung cephalad and become fused backward from the margin with vein R_1; in all but a few generalized members of these three tribes the dichotomous nature of the posterior fork of the sector has been lost by the capture of the anterior branch (R_4) by the stem of the upper fork (R_{2+3}), leaving R_5 alone as the posterior branch of the radial field.

B. In the subfamilies Architipulinae, Tipulinae, Cylindrotominae; and the tribes Lechriini and Limoniini of the Limoniinae, a radial crossvein is present, occupying a *longitudinal* or *oblique* position, and in all higher types becoming part of a serial vein composed of $R_1 + r + R_2$. The distal sections of R_1 and R_2 are lost by atrophy except in the more generalized groups. As in the preceding section A, the *apparent* radial crossvein is really the basal section or deflection of R_2, in the higher groups of the Limoniini this deflection being lost by atrophy. The posterior fork of the primitively dichotomous sector is interpreted as being lost by a fusion of the two elements, R_4 and R_5 to the wing-margin. There is no direct evidence to support this interpretation, however, and it must be held as somewhat tentative (see discussion in concluding paragraph of the Cylindrotominae).

A. *Subfamily Limoniinae: Tribes Pediciini, Hexatomini and Eriopterini.*
1. The cephalization of vein R_2.

In the primitive families of Diptera, the Tanyderidae and Psychodidae, vein R_2 is a full length vein that lies parallel to veins R_1 and R_3 and attains the wing-margin as a separate entity. In all other groups of Diptera, vein R_2 is either connected with R_1 by the longitudinal crossvein r (as discussed in detail under caption B) or has swung cephalad and forms a fusion with R_1 backward from the margin.

As a preliminary to the data that are presented in this paper, the family Tanyderidae should be briefly considered since it is obviously closest to the ancestral type from which the Pediciini and higher Limoniinae have been evolved. The family includes the following genera: *Macrochile* Lw., fossil, Lower Oligocene (Crampton, 1926*b*); *Protoplasa* O.S., 3 Nearctic, 1 Palaearctic species; *Péringueyomyina* Alex. (*barnardi* Alex.), Ethiopian; *Tanyderus* Phil. (*pictus* Phil.), Neotropical; *Radinoderus* Handl., 7 species, chiefly Australian, 1 Neotropical; *Mischoderus* Handl., 4 or 5 valid species, all from New Zealand; *Neoderus* Alex. (*patagonicus* Alex.), Patagonia; and *Nothoderus* Alex. (*australiensis* Alex.) of Tasmania. *Nothoderus australiensis* Alex. was discussed and figured by
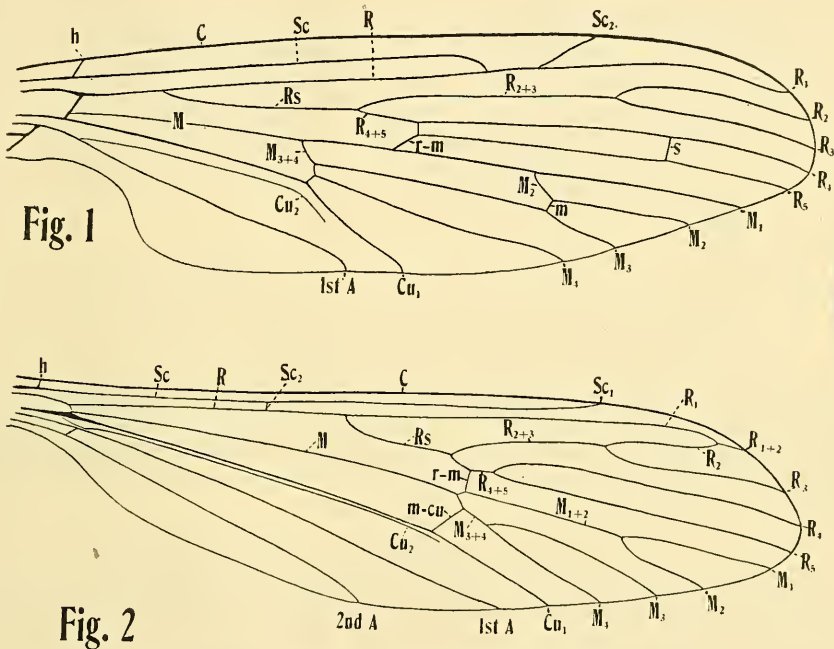
Text-figure 1. Wing of *Nothoderus australiensis* Alex. (Tanyderidae).
Text-figure 2. Wing of *Tricyphona protea* Alex. (Pediciini).
A = anal veins; C = costa; Cu = cubitus; h = humeral crossvein; M = media; m = medial crossvein; m-cu = medial-cubital crossvein; R = radius; r-m = radial-medial crossvein; Rs = radial sector; Sc = subcosta; s = supernumerary crossvein in cell R_4.

MacGillivray (1923, p. 322, fig. 45) as being "the most generalized dipterous wing that I have seen", despite the fact that the free tip of Sc_2, a remarkable feature of the genus, is omitted from his figure. This primitive fly (Text-fig. 1) shows the arrangement of the branches of radius in the Tanyderidae. The supernumerary crossvein (s) in cell R_4 is a feature that is very characteristic of the members of this family and likewise of the Pediciini.

The first realization of the cephalization of vein R_2 in the lower Diptera came to the writer with the discovery of a remarkable crane-fly, *Tricyphona protea* Alex. (Text-fig. 2) where the venation is very like a Tanyderid except that vein R_2 has swung cephalad and fused with R_1 for a short distance back from the wing-margin.

The study of this fly and a comparison with the then known members of the tribe Pediciini resulted in a short paper by the writer (Alexander, 1918) wherein the radial field in this tribe was interpreted about as is done in the present treatment. This interpretation for the Pediciini was adopted by Edwards (1921) and the writer but no attempt was later made to homologize the venation with that of the other tribes in the Limoniinae and Tipulinae and, from them, the phylogenetically higher families of Diptera. A second species of *Tricyphona* (*formosana* Alex., Text-fig. 3) was later discovered in which the venation of this field is about intermediate between *protea* and the normal condition in the tribe (*T. novae-zelandiae* Alex., Text-fig. 4) where this element (the basal section of R_2) is short
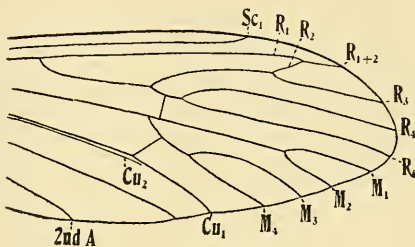
Fig. 3

Fig. 4

Text-figure 3.   Wing of *Tricyphona formosana* Alex.
Text-figure 4.   Wing of *T. novae-zelandiae* Alex.
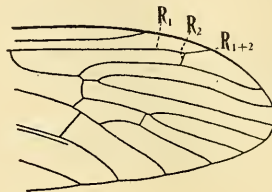
and transverse in position. It is this basal section or deflection of R_2 that has almost universally been interpreted as being r in the groups of Diptera where it has been retained. In a few of his recent papers, the present writer has indicated his opinion that r as a transverse element did not exist in the Tipulidae or in the Diptera.

2. The Capture of Vein R_4 by R_{2+3}.

We now come to one of the most curious features in the problem. In the primitive Diptera (Tanyderidae, Text-fig. 1; *Tricyphona protea* Alex., Text-fig. 2), as elsewhere in generalized groups of the higher orders of insects, the radial sector is typically dichotomously twice forked. In the Tipulidae this dichotomous type has been preserved only in a few scattered groups, chiefly in the Pediciini (Text-figs. 8, 9), and in some Eriopterini (*Molophilus*, Text-fig. 39), the upper fork in all of these types being eliminated by the fusion of the upper branch with R_1, as just outlined. The lower dichotomy in these groups retains its primitive condition of a very deep fork and correspondingly shortened petiole. However, in many members of the tribe under consideration, the Pediciini, as, for example, in the genus *Rhaphidolabis* (Text-figs. 5-6) we find a bewildering condition where the dichotomy is lost by R_4 becoming more intimately attached to the upper fork than to the lower. Similarly in the genera most closely allied to *Molophilus*, as *Erioptera*, we find an entirely comparable condition. This apparently irreconcilable condition is really brought about in a very simple manner by a slight shifting of the relative positions of the veins at the end of the sector. This condition was discussed at some length by Needham in his classic study of the venation of the Tipulidae (1908, pp. 225-226, fig. 14) and has been investigated more superficially by subsequent workers on the family. For the purposes of illustration of the principle,

species of the Pediciine genus *Rhaphidolabis* O.S. in the Nearctic fauna have been selected (Text-figs. 5-9). In species like *R. cayuga* Alex. (Text-fig. 9, 9a) and *R. stigma* Alex. (Text-fig. 8), the primitive condition of the lower fork of the sector is found, cell R_3 being broadly sessile, cell R_4 petiolate. In *R. rubescens* Alex. (Text-fig. 7, 7a) the petiole of cell R_4 has shortened so that both cells R_3 and R_4 appear sessile, vein R_4 being in direct alignment with the sector. From this point on, vein R_4 moves progressively upward on to the stem of the upper fork, R_{2+3}. In *R. major* Alex. (Text-fig. 6, 6a) this migration is very slight so that cell
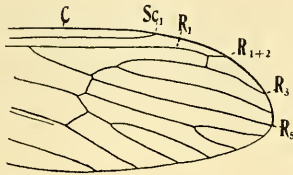
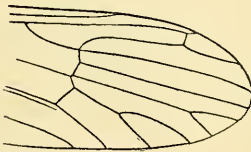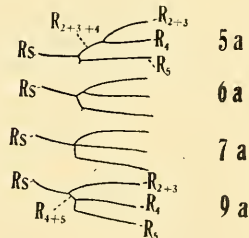Fig. 5
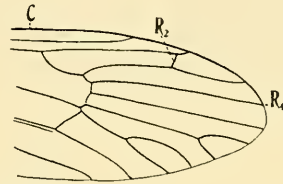
Fig. 8

Fig. 6

Fig. 9

Fig. 7

5 a

6 a

7 a

9 a
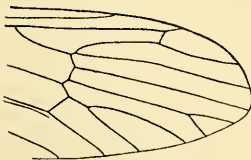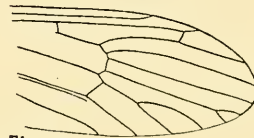
Text-figure 5.   Wing of *Rhaphidolabis polymeroides* Alex.
Text-figure 6.   Wing of *R. major* Alex.
Text-figure 7.   Wing of *R. rubescens* Alex.
Text-figure 8.   Wing of *R. stigma* Alex.
Text-figure 9.   Wing of *R. cayuga* Alex.   Subfigures, 5a, 6a, 7a and 9a, showing details of the forking of the sector in the above species.

R_3 would be described as being short or very short petiolate, the fused vein R_{2+3+4} being this petiole. In still other species, illustrated by *R. polymeroides* Alex. (Text-fig. 5, 5a), the capture of vein R_4 by R_{2+3} has been more complete and the petiole of cell R_3 is conspicuous. Parallel cases are to be found in *Tricyphona* Zett., *Nipponomyia* Alex. (Text-figs. 14-16) and elsewhere in this generalized tribe. The end result of this shifting is the basal fusion of R_{2+3} with R_4 which becomes very extensive in some groups of the family. As the fusion progresses, cell R_3

becomes more shallow until, in cases discussed under the Hexatomini and Eriopterini, it is entirely lost by the fusion to the wing margin of veins R_3 and R_4. After the capture of vein R_4 in the manner described, the single remaining vein of the radial field is R_5.

3. The *Apparent* Radial Crossvein in the Dicranotae.

A few Pediciini (all species of *Dicranota*, *Amalopina dicranotoides* Alex. and *A. sibiriensis* Alex., *Polyangaeus*) possess a crossvein in cell R_1, which, in an earlier paper by the writer (1918, p. 205) was interpreted as being the true *r*. In the light of the evidence now available that *r* in the Diptera, in the relatively few groups where it occurs (as described under caption B, later) always occupies a longitudinal or oblique position and becomes one of the series of elements making up the serial radial vein, it becomes necessary to examine the case in the
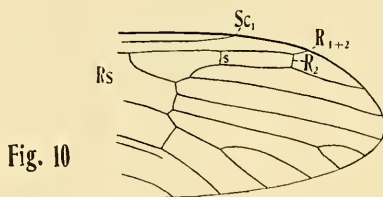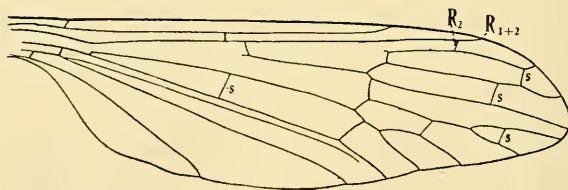

Text-figure 10. Wing of *Dicranota bimaculata* Schumm.
Text-figure 11. Wing *Heterangaeus gloriosus* Alex.
R = radius; Sc = subcosta; s = supernumerary crossveins.

Dicranotae more critically. It should be noted first that this tribe shows a plasticity in the number and position of crossveins, both supernumerary and adventitious, quite unparalleled elsewhere in the Tipulidae, though virtually duplicated in the Tanyderidae. The genus *Heterangaeus* Alex. (Text-fig. 11) shows how abundant these crossveins may be in a single genus and species and there is no reason to believe but that the crossvein in cell R_1, in the cases above outlined, is merely another instance of a supernumerary crossvein, in this case occupying a cell where its position and interpretation becomes far more critical than in the other instances. The plasticity of the character is shown by the fact that *Amalopina dicranotoides* and *A. sibiriensis* are the only ones of the genus (of six species) that possess this supernumerary vein. The genotype, *clegantula*

Brun., lacks this vein but has another in cell R_4. *Dicranota* (Text-fig. 10), in which this character is present, is very closely allied to *Rhaphidolabis* O.S. (Text-figs. 5-9) in which the crossvein is lost, and the presence or absence of this element constitutes the only criterion for the separation of the two groups. Taking into consideration the unusual degree of occurrence of supernumerary and adventitious veins (Johnson, 1901) in members of this tribe, there can be no serious objection to considering the vein in the Dicranotae as being merely an additional supernumerary element stranded in cell R_1.

The writer now wishes to take up the three tribes in this group and discuss the more interesting tendencies.

Pediciini.—As was indicated, the primitive arrangement of the veins at the end of the sector is found in many groups of the tribe. In *Pedicia* Latr., *Ornithodes* Coq., most *Tricyphona* Zett. (Text-figs. 2-4, 12, 13), as well as in *Rhaphidolabis* O.S. (Text-figs. 8-9) the dichotomous arrangement of the veins still obtains. The petiole of the posterior fork (R_{4+5}) is usually short, reaching its maximum length in species
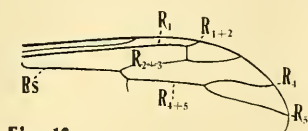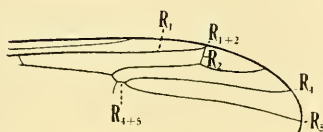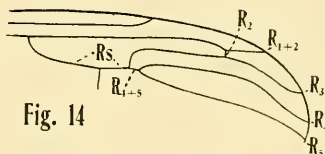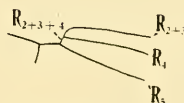

Text-figure 12. Wing of *Tricyphona brevifurcata* Alex.
Text-figure 13. Wing of *T. rainieria* Alex.
Text-figure 14. Wing of *Nipponomyia kuwanai* Alex.
Text-figure 15. The same, showing modification of veins at end of sector.
Text-figure 16. *Nipponomyia symphyletes* Alex.

such as *T. brevifurcata* Alex. (Text-fig. 12). The remarkably primitive condition found in *T. protea* Alex. (Text-fig. 2) has been discussed elsewhere in this paper. No species is definitely known where R_2 ends beyond the level of R_1 and connects directly with costa. In *T. rainieria* Alex. (Text-fig. 13) the deflection of R_2 is at the extreme outer end of vein R_1, as is also the case in *Polyangaeus maculatus* Doane. Doane even figures his type example of this latter species as having this element connected with costa but no mention is made of this very unusual condition in the text and it is presumably erroneous.

The manner in which the dichotomous posterior fork is lost has been discussed earlier in the case of *Rhaphidolabis* (Text-figs. 5-9). A closely comparable case is found in the species of the genus *Nipponomyia* Alex., where the various modifications are found at times in different individuals of the same species. Thus *N. kuwanai* Alex. may have cell R_4 short-petiolate (Text-fig. 14) or sessile (Text-

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fig. 15). *N. symphyletes* Alex. (Text-fig. 16), *N. trispinosa* Alex., *N. novem-punctata* S.-W., and *N. sumatrana* de Meij., have R_4 mounted half-way up the perpendicular basal portion of R_{2+3} so that cell R_3 has become petiolate, cell R_4 broadly sessile. In the genus *Tricyphona* we find a great group of species in which the primitive condition is still retained but in still others (as *inconstans* O.S., *constans* Doane, and many of the European species, as *gmundensis* Egg., *littoralis* Meig., *occulta* Meig., *opaca* Egg., *schineri* Kol., *tipulina* Egg., and others) R_4 has been captured by R_{2+3} in the manner previously described. It should be noted here that occasional specimens of *inconstans* are found that show a reversion to the primitive condition of the genus (Osten Sacken, 1869, p. 267; Johnson, 1901, p. 307). Specimens in the related genus *Pedicia* show a similar range in this field of the wing. As was indicated earlier in this paper, supernumerary crossveins are commonly developed in this tribe, occurring in cells R_1, R_3, R_4 and M in *Polyangaeus* and in cells R_3, R_4, M_1 and M in *Heterangaeus*.

In the subtribe Adelphomyaria, including only the genus *Adelphomyia* Bergr., a connecting element with the following tribe, the Hexatomini, is found. The adult flies are very Hexatomine in structure but the larvae exhibit some curious Pediciine characters. The venation of the radial field is not different from *Limnophila*, discussed later, except that the basal section of R_2 is often weakly developed and tends to be lost by atrophy.

Hexatomini. This tribe is apparently naturally derivable from the Pediciini through the Adelphomyaria on the one hand, and the lowermost subtribe, the Ularia, on the other. Within the tribe there is found a remarkable range of usually large to medium-sized species that are arranged in a variety of subtribes. The number of these latter sub-divisions will probably be increased when certain doubtful genera become better known and new types are discovered. The most specialized groups appear to fall in the Gynoplistiaria, the Limnophilaria, the Hexatomaria and the Elephantomyaria, some of which lead rather gradually toward the Eriopterini. The chief modifications and tendencies in the radial field are discussed below.

Ularia. Includes only the genus *Ula* Haliday. The venation is not different from some species of *Tricyphona*, as *inconstans* O.S.

Epiphragmaria. Includes a number of chiefly Antipodal genera, as *Epiphragma* O.S., *Polymoria* Phil., *Limnophilella* Alex., *Acantholimnophila* Alex., *Rhamphophila* Edw., *Tinemyia* Hutt., *Phyllolabis* O.S., *Horistomyia* Alex., *Heterolimnophila* Alex., *Polymera* Wied., and others. The venation shows no modifications of the radial field over that of *Gynoplistia*, described later.

In *Polymera*, the position of the basal section of R_2 differs greatly in the various species, in some, as *inornata* Alex., the last section of R_1 being equal to R_{1-2} while in other species the section of R_2 is far out toward the tip of R_1.

Pseudolimnophilaria. Includes only the genus *Pseudolimnophila* Alex., as known, but other groups will probably be added to the subtribe when better known. The genus included is not different in venation from *Limnophila*.

Dactylolabaria. Includes only the genus *Dactylolabis* O.S., so far as known. As before, the venation is normal for the Hexatomini and requires no comment.

Gynoplistiaria. Includes only the genus *Gynoplistia* Westw., with four subgeneric groups, *Paralimnophila* Alex., *Gynoplistia, Cerozodia* Westw., and *Ctedonia* Phil. The group is tremendously developed in Australia and New Zealand. The figure of *G. bella* Walk. (Text-fig. 17) may be taken as typical not only of the subtribe but for the entire tribe Hexatomini. R_{2+3+4} is almost always

very short to entirely obliterated (as in *G. dimidiata* Alex., *G. harrisi* Alex., *G. hiemalis* Alex., *G. nigronitida* Alex.), cell R_3 thus varying from short-petiolate to sessile; R_{2+3} elongate, usually perpendicular or subperpendicular at origin, sometimes with a short spur or weak crossvein at the angle; basal section of R_2 short, the fused R_{1+2} generally short to of moderate length.

   Limnophilaria. This subtribe as now constituted includes a considerable range of genera, some of which are discordant and will later be removed. A few of the groups require special comment. *Psaronius* End. shows a venational range
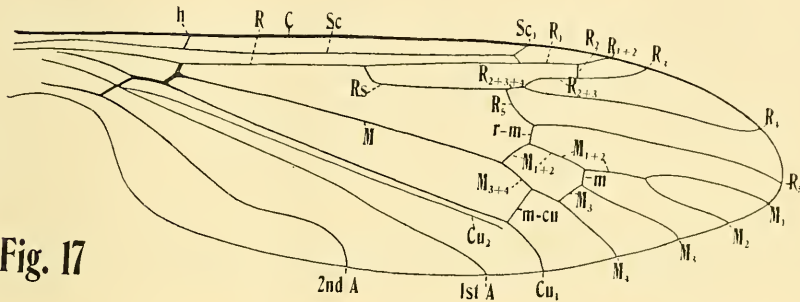
Text-figure 17. Wing of *Gynoplistia bella* Walk.

of the radial field that closely parallels that of the Eriopterine genera *Paragymnastes* and *Gymnastes*. Rs is long and lies close to R_1 in alignment with R_{2+3+4} and its continuation, R_4; even in the most generalized species, as *obscurus* Fabr. (Text-fig. 18), R_{2+3} is relatively short and R_3 weak although long and lying parallel to the fused R_{1+2}. In *trianguliferus* Alex. (Text-fig. 19) the tip of R_3 has swung basad and is fused with the tip of R_{1+2}, cell R_2 being elongate-triangular.
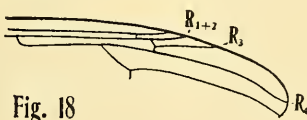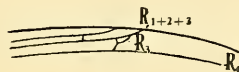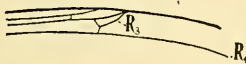

Text-figure 18. Wing of *Psaronius obscurus* Fabr.
Text-figure 19. Wing of *P. trianguliferus* Alex.
Text-figure 20. Wing of *P. obliteratus* Alex.
Text-figure 21. Wing of *P. abnormis* Alex.

In *obliteratus* Alex. (Text-fig. 20) the fusion backward from the tip has proceeded so far that cell R_2 is reduced to a tiny triangle. In species such as *abnormis* Alex. (Text-fig. 21), *brevitibia* Alex., and *mancus* Alex., the tendency is carried to its logical conclusion and cell R_2 is entirely obliterated.

The genus *Ischnothrix* Bigot is of importance as indicating the manner in which the aberrant genus *Atarba* O.S. has been derived. In *I. australasiae* Skuse (Text-fig. 22) R_{2+3+4} is very long, the branches R_3 and R_4 short but separate, cell
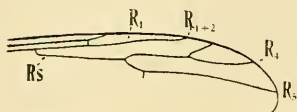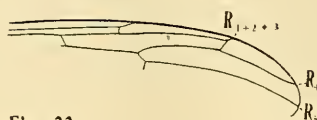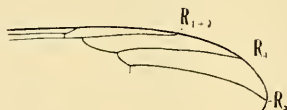

Fig. 22

Fig. 23

Fig. 24

Text-figure 22. Wing of *Ischnothrix australasiae* Skuse.
Text-figure 23. Wing of *I. connexa* Alex.
Text-figure 24. Wing of *Atarba picticornis* O.S.

R_3 being small. In still other species, as *I. connexa* Alex. (Text-fig. 23) a secondary modification is produced by R_3 having swung basad and fusing backward from the margin with R_{1+2}, presumably for the purpose of strengthening this field of the wing. Similar cases are found in the Eriopterine genus *Gonomyia*, subgenus
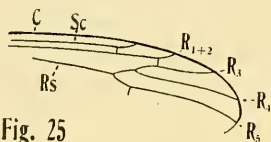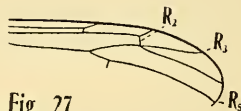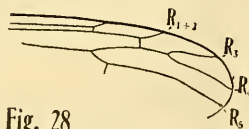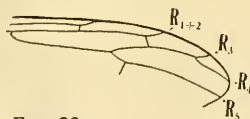

Fig. 25

Fig. 27

Fig. 26

Fig. 28

Fig. 29

Text-figure 25. Wing of *Eriocera velveta* Doane.
Text-figure 26. Wing of *E. wilsoni* O.S.
Text-figure 27. Wing of *E. gibbosa* Doane.
Text-figure 28. Wing of *E. fultonensis* Alex.
Text-figure 29. Wing of *Hexatoma megacera* O.S.

Ptilostena Bergr. In *Atarba* (*picticornis* O.S., Text-fig. 24) veins R_3 and R_4 have fused to the wing-margin or, possibly, one of the branches atrophied shortly before the margin.

Hexatomaria. This very extensive and important subtribe includes four very closely allied genera, *Eriocera* Macq., *Penthoptera* Schin., *Hexatoma* Latr., and *Cladolipes* Lw. Members of this subtribe are chosen to illustrate the manner in which veins R_{2+3} and R_4 fuse to the wing-margin in certain groups of Hexatomini and Eriopterini. The figures show a series of Nearctic species of *Eriocera*, with one species of *Hexatoma*. In *E. velveta* Doane (Text-fig. 25) cell R_3 is still very deep; in *E. wilsoni* O.S. (Text-fig. 26) the cell is a little shorter in proportion to its petiole; *E. gibbosa* Doane (Text-fig. 27) shows the fusion as having progressed to opposite the point of departure of the basal section of R_2; *E. fultonensis* Alex. (Text-fig. 28) shows the fusion of R_3 and R_4 as having continued to some distance beyond R_2; *Hexatoma megacera* O.S. (Text-fig. 29) has the veins fused almost to the margin. The condition results in a complete fusion in the European *Cladolipes simplex* Lw. The deepest cell in this subtribe known to the writer is in *E. subrectangularis* Alex., where R_{2+3+4} is about as long as *r-m*.

Elephantomyaria. The very aberrant genus *Elephantomyia* O.S. (*westwoodi* O.S., Text-fig. 30) is placed in the Hexatomini with some question although the reference seems to be correct. The genus as interpreted shows veins R_3 and R_4
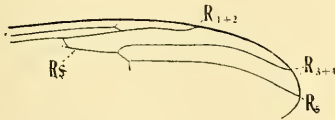

Fig. 30   Fig. 31

Text-figure 30.   Wing of *Elephantomyia westwoodi* O.S.
Text-figure 31.   Wing of *E. major* Alex.

fused to the wing-margin and the basal section of R_2 entirely atrophied. In the subgenus *Elephantomyodes* Alex., of the Indo-Australian Region (*major* Alex., Text-fig. 31), R_{2+3+4} at origin is perpendicular to subperpendicular, the distal section being closely approximated to R_1.

In the tribe Hexatomini, the basal section of R_2 is lost by atrophy in many genera, as *Horistomyia leucophaea* Skuse, *Phyllolabis* O.S., some *Zelandomyia* Alex., *Harrisomyia* Alex., *Ischnothrix* Big., *Elephantomyia* O.S., and others. A few groups show a supernumerary crossvein in cell R_3, as *Ctenolimnophila* Alex. (*decisa* Alex.); the subgenus *Calolimnophila* Alex., of *Pseudolimnophila* Alex.; the subgenus *Dicranophragma* O.S. of *Limnophila* Macq.; *Elephantomyia supernumeraria* Alex., and others. In *Ctenolimnophila bivena* Alex., there is an additional supernumerary crossvein in cell R_4.

Eriopterini. The great tribe Eriopterini has evidently been derived from the Hexatomini through certain of its subtribes, as the Claduraria and Conosiaria which have retained numerous Hexatomine features and have been referred to as the "Hexatomoid Eriopterini." The most generalized subtribes would thus be those just mentioned, leading, through the Gonomyaria to the so-called "pot-bellied" Eriopterini, the typical Eriopteraria. · In this vast assemblage of genera and subgenera several specializations and modifications from the normal type are found that are very puzzling and difficult of explanation. The greatest trouble comes in

three, chiefly Ethiopian, genera, *Ceratolimnobia*, *Xipholimnobia* and *Xenolimnobia*, which, as discussed later, may well pertain to the Lechriini in the following group of subfamilies. More material will be needed to determine finally the exact systematic position of many of the crane-fly genera and a critical study of all the stages and available structures must be made. Very many of the larger and more widely distributed genera are vastly ancient and there has been almost unlimited time during which the various modifications and tendencies have been evolved. It is very certain that more subtribes will be formed when certain groups of exotic Eriopterini become better known. In many of the higher members of the tribe, the basal section of R_2 has atrophied, leaving no hint as to its exact former position. When present, this element shows a great range in position, in some, as *Molophilus* (Text-fig. 39) and *Erioptera* (Text-fig. 40) being retreated far from the tip of R_1, the fusion of R_1 and R_2 thus being very extensive; in still others the element is far out toward the end of vein R_1. When the element has atrophied, as in *Gonomyia* and many other groups, all that can be affirmed is that the distal section of R_2 has fused with R_1 and the vein at the margin must be called R_{1+2}.

In the present paper, only a few of the more conspicuous types and certain modifications can be discussed.

Claduraria. This subtribe includes *Cladura* O.S., *Neocladura* Alex., *Crypteria* Bergr., *Pterochionea* Alex., *Neolimnophila* Alex., and *Chionea* Dalm., a group of genera very characteristic of the northern Holarctic Region, most of them appearing as adults in autumn and winter. The venation shows no modifications from the normal type of the Hexatomini and is not further discussed.

Conosiaria. Includes *Conosia* v.d.W. and *Clydonodozus* End., two closely allied Palaeotropical genera in which the maxillary palpi are greatly reduced. The more generalized genus, *Clydonodozus*, has the basal section of R_2 transverse and not greatly different from the condition in the Hexatomini (*angustifasciatus* Alex., Text-fig. 32). The more specialized genus, *Conosia* (*irrorata* Wied., Text-
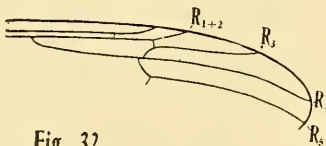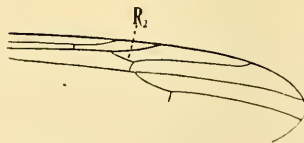

Text-figure 32. Wing of *Clydonodozus angustifasciatus* Alex.
Text-figure 33. Wing of *Conosia irrorata* Wied.

fig. 33) has the basal section of R_2 reflexed back toward the wing-base so that the proximal end of cell R_2 is acutely pointed. It should be noted that the shifting of veins at the end of Rs, as already discussed in some detail for the Pediciini, is found in these two genera and even in different specimens of the single genus *Conosia*.

Gonomyaria. An extensive subtribe, interpreted as including, among others, *Gonomyia* Meig., *Gnophomyia* O.S., *Teucholabis* O.S., *Trentepohlia* Big., *Paragymnastes* Alex., *Gymnastes* Brun., *Campbellomyia* Alex., *Dasymallomyia* Brun., *Lipsothrix* Lw., *Aphrophila* Edw., *Astelobia* Edw., *Austrolimnobia* Alex., *Sigmatomera* O.S., *Lecteria* O.S., *Platylimnobia* Alex., and more doubtfully, *Ceratolimnobia* Alex., *Xipholimnobia* Alex. and *Xenolimnobia* Alex.

The following groups should be more critically examined to determine their strict position in subtribes; (1) *Trentepohlia*; (2) *Sigmatomera, Astelobia, Austrolimnobia*; (3) *Lecteria* (and its exact relationships with the Hexatomine genus *Psaronius*); (4) *Paragymnastes* and *Gymnastes*; (5) *Aphrophila*; and (6) *Ceratolimnobia, Xipholimnobia* and *Xenolimnobia*. The genera as listed above are grouped chiefly on thoracic characters and, as so united, unquestionably include some discordant elements.

Most of the groups require no special explanation to homologize their venation with the groups previously discussed. In *Trentepohlia* and *Astelobia*, the basal section of R_2 is reflexed strongly basad, as in *Conosia*, just described. The allied genus *Austrolimnobia* has the element transverse and normal in position. In *Paragymnastes* (*fascipennis* Thoms., Text-fig. 34) and *Gymnastes* Brun. (*ornatipennis* de Meij., Text-fig. 35, *shirakii* Alex., Text-fig. 36) we find the loss of the free distal section of R_3 by gradual atrophy and probable fusion back from
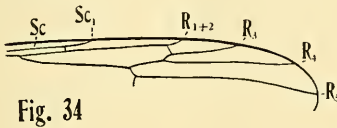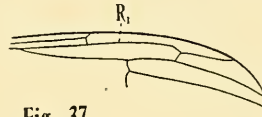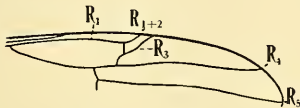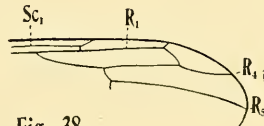

Fig. 34

Fig. 37

Fig. 35

Fig. 38

Fig. 36

Text-figure 34. Wing of *Paragymnastes fascipennis* Thoms.
Text-figure 35. Wing of *Gymnastes ornatipennis* de Meij.
Text-figure 36. Wing of *G. shirakii* Alex.
Text-figure 37. Wing of *Xipholimnobia terebrina* Alex.
Text-figure 38. Wing of *Xenolimnobia camerounensis* Alex.

the tip of R_{1+2}, much as previously described under the Hexatomine genus *Psaronius*. In *Gonomyia* and *Teucholabis* we find a progressive increase in the degree of fusion of veins R_3 and R_4, in exactly the same manner as discussed under *Eriocera* (Text-figs. 25-29) in the preceding tribe. This culminates in the subgenera *Lipophleps* Bergr. and *Teucholabis*, respectively, cell R_3 being obliterated, producing a venation that is very similar to that found in the Limoniini in the next section. In *Teucholabis*, *r-m* is sometimes obliterated by the fusion of vein R_5 on M_{1+2}.

In *Ceratolimnobia* and allied genera, as mentioned above, a much more difficult and serious problem is found. In *Ceratolimnobia* and *Xipholimnobia* (*terebrina* Alex., Text-fig. 37) the appearance is much as in *Trichoneura*, that has been placed in the Lechriini of the following section, except that the critical

distal section of R_1 is not preserved in any material that has been discovered and the apparent homology may be apparent only. In *Xenolimnobia* (*camerounensis* Alex., Text-fig. 38) the condition is reversed, the apparent tip of R_1 being preserved but the entire distal section of R_2 atrophied. It is greatly hoped that additional and possibly annectant forms in this group will be discovered.

Eriopteraria. This subtribe is restricted to the so-called "pot-bellied" Eriopterini (Crampton, 1925, p. 199) and includes among others, the following genera: *Erioptera* Meig., *Empeda* O.S., *Psiloconopa* Zett., *Cryptolabis* O.S., *Dasymolophilus* Goetg., *Tasiocera* Skuse, *Molophilus* Curt., *Ormosia* Rond., *Amphineurus* Skuse, *Trimicra* O.S., *Helobia* St. Farg., *Podoneura* Bergr., *Empedomorpha* Alex., and *Rhabdomastix* Skuse. The species of *Rhabdomastix* bear a noteworthy resemblance to *Gonomyia*, with which genus they were long confused in the European fauna. The genus entirely parallels *Gonomyia* in that some few generalized species have retained the basal section of R_2 while in the majority it is entirely atrophied. In all of the species of the genus yet made known, cell R_3 is present though often very small.

In *Molophilus* (*froggatti* Skuse, Text-fig. 39) we find the same generalized dichotomy of the sector that has been considered under the Pediciini. An intermediate condition is found in *Dasymolophilus* and, especially, in several New Zealand species of *Amphineurus* where cell R_3 ranges from barely sessile through other species where the cell is short-petiolate, to *Erioptera* (*lutea* Meig., Text-fig.
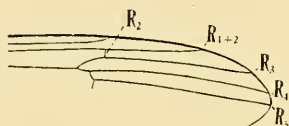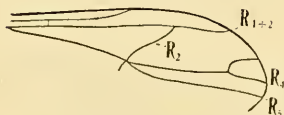

Fig. 39

Fig. 40

Fig. 41

Fig. 42

Text-figure 39. Wing of *Molophilus froggatti* Skuse.
Text-figure 40. Wing of *Erioptera lutea* Meig.
Text-figure 41. Wing of *Empedomorpha empedoides* Alex., ♂.
Text-figure 42. Wing of *Styringomyia terrae-reginae* Alex.

40) where the cell is distinctly petiolate. A curious modification of the veins of the radial field in the male of *Empedomorpha* (*empedoides* Alex., Text-fig. 41) is found where the basal section of R_2 is very long, the other elements being reduced and crowded. The female of the same species is a very ordinary fly.

Styringomyini. The single very isolated genus *Styringomyia* Lw. (*terrae-reginae* Alex., Text-fig. 42) is placed here. The venation of the radial field some-

what suggests *Ceratocheilus*, as discussed under the following section, R_{2+3} being very short and lying obliquely, far distad of R_1. Any discussion as to how this remarkable venation might have been evolved would be theoretical only.

B. *Subfamilies Architipulinae, Tipulinae and Cylindrotominae; Subfamily Limoniinae: Tribes Lechriini and Limoniini.*

1. The serial nature of vein R_1.

The term *serial vein* was proposed by Comstock (1918, p. 69) for a compound vein composed of sections of two or more veins joined end to end with no indication of the point of union. In the subfamilies and tribes considered under this caption, the vein that has hitherto been called R_1 (Needham, 1908; Comstock, 1918) is, in reality, such a serial vein, being composed of three distinct elements, R_1, r, and the distal section of R_2. At the margin the vein should be labelled as being R_2 alone (except in the cases noted below), and the cell beneath this distal section of R_2 should be called R_2 instead of cell 2nd R_1 as heretofore. In the Tipulinae, Cylindrotominae, Lechriini and the more generalized Limoniini, the three elements constituting the distal end of this serial vein still preserve much of their separate identity by a more or less zig-zag arrangement, and, in many cases, by the preservation of the free tips of veins R_1 and R_2. The former of these elements is lost in some Cylindrotominae and most Limoniini but is preserved in virtually all Tipulinae, the Lechriini and some generalized Limoniini. The latter element, R_2, is lost in many Tipulinae (as the Dolichopezaria, many *Tipula*) and in the majority of the Cylindrotominae but is preserved and forms the true end of this serial vein in many Limoniini, but not in the subtribe Limoniaria, as discussed later. Veins R_4 and R_5 are interpreted as having fused to the margin, the resulting vein being R_{4+5}.

Architipulinae. The family Architipulidae, proposed by Handlirsch (1906-08, pp. 490-491) represents at most a valid subfamily of the Tipulidae. Of the genera placed therein by Handlirsch, only *Architipula* Handl. belongs here, the others (*Protipula* Handl., *Eotipula* Handl.) being either Limoniinae or Trichoceridae. All three genera pertain to the Upper Liassic, of an approximate age of 140,000,000 of years (Lane, 1919). The genera and species referred to the Eoptychopteridae in the same reference are more problematical and no attempt is made herein to correlate this material.

Tipulinae. The primitive condition of the radial field in the Tipulinae must be assumed as being much as in the Architipulinae, that is, with cell R_2 deeper than in recent genera, though approached by some species of Ctenophoraria (*Ctenophora* Meig., *Cnemoncosis* End., and *Tanyptera* Latr., *fumipennis* O.S., Text-fig. 43). Other genera of this subtribe show the cell less elongate, as *Prionota* v.d.W., *Pselliophora* O.S., *Dictenidia* Brullé, and some *Ctenophora* and *Tanyptera*. The generalized condition likewise assumes that the distal sections of veins R_1, R_2 and R_3 are entire and that the true radial crossvein, r, is present, connecting R_{2+3} at the fork or R_2 shortly beyond the origin. It should again be emphasized that this radial crossvein is never transverse in position but always longitudinal or oblique, forming part of the more or less zig-zag serial vein in this subfamily. The homologies of the radial field are more obvious than in any other group of the Tipulidae and there has been little dispute as to the correct terminologies in this field of the wing. Comstock (1918, fig. 377; 1924, fig. 1009) has labelled the basal section of R_2 as being r.

The following, chiefly Australasian genera show a primitive type of radius, in most of them vein R_3 being very long and extended, greatly exceeding R_2: *Clytocosmus* Skuse (*skusei* Alex., Text-fig. 44); *Platyphasia* Skuse; *Ptilogyna* Westw., *Phacelodocera* End., *Plusiomyia* Skuse (*felix* Alex., Text-fig. 45);
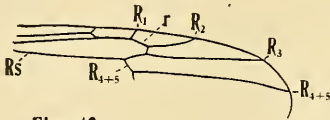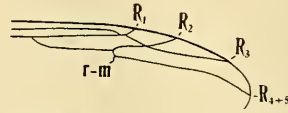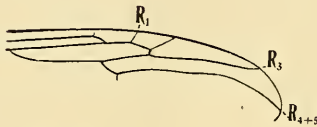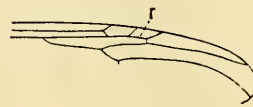

Fig. 43

Fig. 44

Fig. 45

Fig. 46

Text-figure 43.   Wing of *Tanyptera fumipennis* O.S.
Text-figure 44.   Wing of *Clytocosmus skusei* Alex.
Text-figure 45.   Wing of *Plusiomyia felix* Alex.
Text-figure 46.   Wing of *Leptotarsus macquarti* Guer.

Ozodicera Westw., *Leptotarsus* Guer. (*macquarti* Guer., Text-fig. 46); *Semnotes* Westw., *Acracantha* Skuse; *Ischnotoma* Skuse; *Habromastix* Skuse; *Phymatopsis* Skuse; *Macromastix* O.S.; *Hudsonia* Edw.; *Zelandotipula* Alex.; *Longurio* Lw. and *Tipulodina* End.

In some species of *Acracantha, Ischnotoma, Hudsonia*, and the genera of the higher Tipularia (*Prionocera* Lw., *Holorusia* Lw.; *Ctenacroscelis* End.; *Pectinotipula* Alex.; *Tipula* Linn. and *Nephrotoma* Meig.), *r* is somewhat more
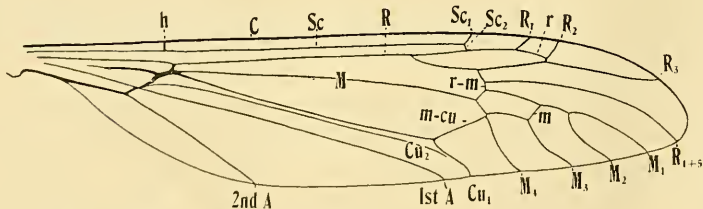

Fig. 47

Text-figure 47.   Wing of *Macromastix costalis* Swed.

oblique in position and cell R_2 is smaller, vein R_3 being much less extended. *Holorusia, Ctenacroscelis* and *Zelandotipula*, moreover, have vein R_3 very strongly arcuated toward vein R_{4+5}, strongly constricting cell R_3.

In *Brachypremna* O.S. (*candida* Alex., Text-fig. 48), *Tanypremna* O.S., *Megistocera* Wied. (*longipennis* Macq., Text-fig. 52), some *Macromastix* O.S. (*costalis* Swed., Text-fig. 47) and others, the free tip of R_2 tends to become transverse or nearly so.

Aldrovandia End. (*gesneri* End., Text-fig. 53) has *r* and the very long basal section of R_2 in oblique alignment, the distal section of R_2 being relatively short and paralleling R_1, R_3 being very extended.

In most of the genera that have been assigned to the Dolichopezaria (*Dolichopeza* Curt., Text-figs. 49-51; *Oropeza* Ndm.; *Nesopeza* Alex.; *Scamboneura* O.S.; *Megisto-mastix* Alex.) and other genera in the Tipularia (as *Microtipula* Alex.; *Idiotipula* Alex.;
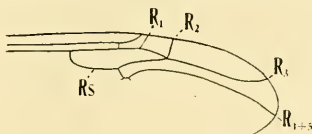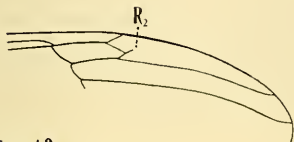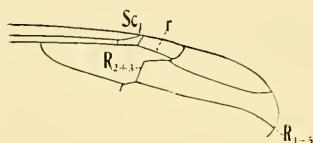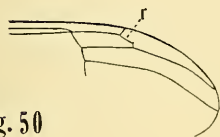
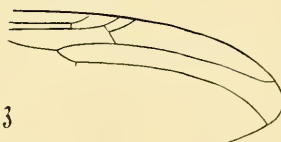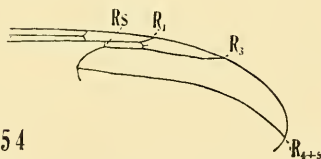

Fig. 48

Fig. 49

Fig. 52

Fig. 50

Fig. 53

Fig. 51

Fig. 54

Text-figure 48. Wing of *Brachypremna candida* Alex.
Text-figure 49. Wing of *Dolichopeza malagasya* Karsch.
Text-figure 50. Wing of *D. cinerea* Macq.
Text-figure 51. Wing of *D. queenslandica* Alex.
Text-figure 52. Wing of *Megistocera longipennis* Macq.
Text-figure 53. Wing of *Aldrovandia gesneri* End.
Text-figure 54. Wing of *Scamboneura plumbea* Alex.

Xenotipula Alex.; *Tipula* (*Acutipula*) *omissinervis* de Meij., and numerous species of the genus *Tipula*, chiefly in the Holarctic Region) the distal section of R_2 is entirely or partly atrophied. When the former is the case, as in many *Dolichopeza* (*queenslandica* Alex., Text-fig. 51) and others, the resulting vein that connects R_1 and R_3 is a serial vein, the cephalic portion being *r*, the usually much shorter posterior portion the basal section of R_2. In other cases, as the subgenus *Trichodolichopeza* Alex., the alignment is not so perfect. In *D. malagasya* Karsch (Text-fig. 49), the basal section of R_2 forms an acute angle with *r* and the basal portion of the distal section of R_2 is preserved as a short stub. A less accentuated case is found in some specimens of *Dolichopeza* (*cinerea* Macq., Text-fig. 50) and many of the species of *Tipula*, above mentioned.

The radial sector, short and transverse in genera such as *Dolichopeza* (Text-figs. 50-51) and *Nephrotoma*, reaches its minimum size in *Scamboneura* O.S. (*plumbea* Alex., Text-fig. 54) where it has apparently migrated distad beyond the level of the other elements of the cord so that it lies at the proximal end of the stigma and appears to be a short supernumerary crossvein; R_{2+3} is then given off, paralleling vein R_1 and forming the caudal margin of the stigma, the tips of veins R_1, R_2 and R_3 are not especially abnormal but are greatly reduced in size and much crowded. The basal section of R_{4+5} is lengthened and directed strongly basad to form the cephalic portion of the cord. There is a strong spur, sometimes at the angle of R_{4+5} and *r-m*, in other cases on *r-m* itself, jutting basad into cell R. There is an alternative interpretation to the above that is not as satisfactory since it does not explain the small transverse element above interpreted as being the radial sector. This interpretation would call for an elongated sector that is almost entirely atrophied except for the small spur that juts basad into cell R, as described. It is probable that more conclusive evidence will not be long in coming as material in the genus *Scamboneura* is not especially rare in certain Malayan islands, especially the Philippines.

In *Ptilogyna*, vein R_{4+5} fuses with M_{1+2}, obliterating *r-m*.

Cylindrotominae. The primitive type of the Cylindrotominae may be assumed as having been not unlike the fossil genus *Cyttaromyia* Scudd. (1894, p. 190), with the retention of the distal sections of veins R_1 and R_2 that have been lost in *Cyttaromyia* and many of the living species of the group. When the fauna of the world is considered, several species are found that have retained one or the other of these two branches. An earlier interpretation of the venation of the Cylindrotominae (Needham, 1908) called for a long fusion of the veins back from the wing-margin. The true interpretation of this field was given by Osten Sacken (1869, pp. 290-291) and later amplified by the writer (Alexander, 1914, pp. 604-605; 1919, p. 863). Brunetti (1918, pp. 280-283) has discussed the problem of the venation in the group but has failed to appreciate the true homologies of the veins (as is shown by his still calling the basal section of R_2 in *Phalacrocera replicata* the marginal crossvein, *r*, and the distal section of R_1 the "costal crossvein"). Brunetti has summed up his beliefs in the following words: "I contend it must be admitted that the 1st vein (R_1) normally and actually ends in the second (base of R_2 or R_{2+3}) because whenever the costal crossvein (distal section of R_1) is absent it most obviously does so end". The venational symbols in parentheses are supplied by the present writer. There can be little question but that the Cylindrotominae have been derived from some Tipuline ancestor in middle or late Mesozoic times.

The following modifications in the various genera may be noted: *Cylindrotoma* Macq. (*nigriventris* Lw., Text-fig. 55) retains the primitive condition of the group except that the distal section of R_2 is entirely atrophied. In a few species (as *splendens* Doane), the distal section of R_1 is only weakly preserved or even atrophied, though present in most individuals. *Phalacrocera* Schin. is of especial importance in that the more generalized species (*replicata* Linn., Text-fig. 56) have retained all three branches of this region of the wing, although R_1 is represented only by a weak spur, *r* in this case being very long as compared with other species of the genus. In more specialized cases (*tipulina* O.S., Text-fig. 57, *occidentalis* Alex.) the tip of R_2 is entirely atrophied. In *P. formosae* Alex., the tips of both R_1 and R_2 are quite atrophied. *Liogma* O.S. has the genotype, *nodicornis* O.S., with the tips of both R_1 and R_2 atrophied. The other species agree

in this respect but some specimens of *glabrata* Wied. retain R_1 as a weak element. In *Triogma* Schin., R_1 is strongly preserved in *exculpta* O.S., weakly preserved in *trisulcata* Schumm., lacking in *kuwanai* Alex.

In *Stibadocera* End. (*metallica* Alex., Text-fig. 58), R_{2+3} diverges widely from R_{4+5} and is shorter to much shorter than R_3 alone. The distal section of R_1 is preserved but that of R_2 is entirely atrophied. *Stibadocerella* Brun. (= *Agastomyia* de Meij.) shows no trace of the distal sections of either R_1 or R_2. *Stibadocerodes* Alex. (*tasmaniensis* Alex., Text-fig. 59) shows no vestige of the distal section of R_1, the extreme base of the distal section of R_2 being more or less preserved as a
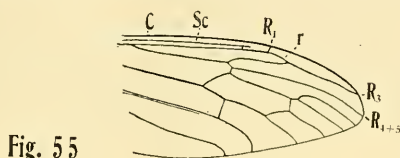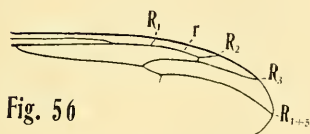

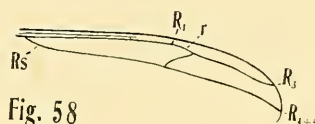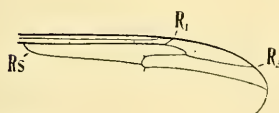Text-figure 55. Wing of *Cylindrotoma nigriventris* Lw.
Text-figure 56. Wing of *Phalacrocera replicata* Linn.
Text-figure 57. Wing of *P. tipulina* O.S.
Text-figure 58. Wing of *Stibadocera metallica* Alex.
Text-figure 59. Wing of *Stibadocerodes tasmaniensis* Alex.

short spur, that, when present, is provided with macrotrichiae. The fusion of R_{2+3} is very long, exceeding R_3 alone, and the space between Sc_2 and the basal section of R_2 (the combined penultimate section of R_1 and r) is correspondingly lengthened; r-m unites with Rs before (*australiensis* Alex.) or at the fork.

In a few genera of Cylindrotominae, R_{4+5} has swung caudad and fused for a greater or less extent with M_{1+2}, obliterating r-m (some *Liogma*, *Triogma*).

It may be noted in concluding this brief account of the subfamily that the more primitive members of the group (*Cyttaromyia*, *Cylindrotoma*) may provide the explanation of the fate of the posterior fork of the sector in this group of subfamilies. As has already been noted this has been called a fusion of veins R_4 and R_5 to the margin. There is a possibility, however, that the branch interpreted as being M_1 may represent R_5 of the primitive type. In *Cyttaromyia* this is always connected strongly with R by a crossvein or *apparent* crossvein at near

midlength of the cell and in many examples of *Cylindrotoma* this position is still indicated by a strong spur at the angle of M_1. It is not impossible that in the progressive outward fusion of R_4 and R_5 in this group of subfamilies that the latter vein in the ancestral type was deflected caudad and became fused or intimately connected with M.

Lechriini.   This new group includes the genera *Lechria* Skuse and *Trichoneura* Lw. *Lechria* was placed in the tribe Eriopterini by Skuse despite the presence of distinct tibial spurs.   Later, the genus was removed to the Hexatomini (de Meijere, Alexander).   *Trichoneura* was described from the Baltic Amber (Lower Oligocene) but has since been found living in the Himalayas.

Lechria (*sublaevis* Alex., Text-fig. 60) has *r* long, gently arcuated, connecting with R_2 some distance from the origin of the latter.   *L. singularis* Skuse is figured by its describer as having *r* connecting with R_{2+3} immediately at the fork but a photograph of the wing of the type kindly made for me by Mr. John Shewan shows
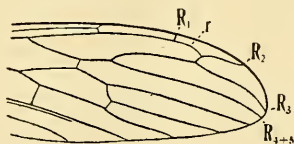

Fig. 60   Fig. 61
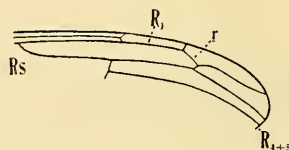
Text-figure 60.   Wing of *Lechria sublaevis* Alex.
Text-figure 61.   Wing of *Trichoneura vulgaris* Lw.

that this species, like the above, has *r* connecting with R_2 shortly beyond the origin, forming a short basal section.   The *r-m* crossvein is on Rs far before the fork.

Trichoneura (*vulgaris* Lw., Text-fig. 61) presents a more normal Hexatomine appearance, *r-m* being connected with R_{4+5} shortly beyond the origin.

Until the present writing both of the above genera have been referred to the Hexatomini.   The similarity of the venation to other Hexatomine genera must be explained by convergence.   An entirely comparable case is found in the genus *Trichocera* Meig., which until very recently was placed with *Limnophila* in the Hexatomini, the venation of the two groups being entirely comparable.   It is now known that *Trichocera* represents an entirely distinct family of Diptera (Alexander, 1926).

As was indicated under the account of the Eriopterini, the genera *Ceratolimnobia*, *Xipholimnobia* and *Xenolimnobia* discussed at that time may correctly pertain to the present group.

Limoniini.   In the tribe Limoniini, the elements of the serial vein have become straightened out in perfect alignment or nearly so.   In its typical condition, as shown by the subtribe Orimargaria, the venation of the radial field is not difficult to homologize with the entirely similar conditions obtaining in the Tipulinae, Cylindrotominae or the Lechriini, previously considered.   In the higher subtribes, especially in the Limoniaria, a very puzzling modification is

brought about in the various species by an outward shifting of the free tip of R_1, a condition that is discussed in detail under the account of the subtribe.

Some of the more aberrant subtribes that were formerly arranged in the old tribe Antochini before its partition are placed in this tribe rather arbitrarily while awaiting more data to determine their final disposition. Such genera are *Antocha, Orimargula, Orimarga, Diotrepha, Thaumastoptera, Elliptera, Helius, Toxorhina* and *Dicranoptycha*. The position of *Toxorhina* in this tribe is most in doubt. Of the other generic groups placed by Osten Sacken in the Antochini (as Limnobina anomala), *Teucholabis* has already been discussed under the Eriopterini, and *Atarba* and *Elephantomyia* under the Hexatomini. Professor Rogers has recently reared *Atarba* and some features of its life-history point strongly to the present tribe but the affinities of the genus with *Ischnothrix* are very marked and the group requires further study. The true status of many of these aberrant subtribes of the Limoniini will probably remain long in dispute and will be solved finally only by a knowledge of all the stages and, perhaps, the discovery of other and annectant types.

Orimargaria. This subtribe includes *Orimarga* O.S. and *Diotrepha* O.S., the two genera being closely allied and showing entirely comparable modifications of
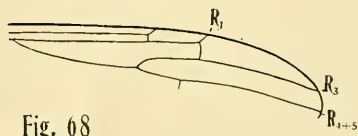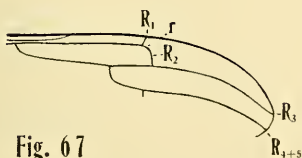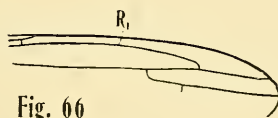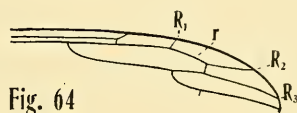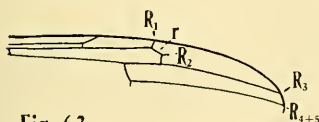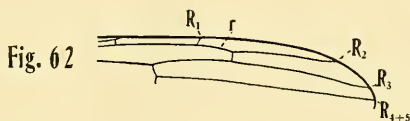
Text-figure 62.   Wing of *Orimarga excessiva* Alex.
Text-figure 63.   Wing of *O. punctipennis* Alex.
Text-figure 64.   Wing of *Diotrepha fumicosta* Alex.
Text-figure 65.   Wing of *Orimarga joana* Alex.
Text-figure 66.   Wing of *Diotrepha atribasis* Alex.
Text-figure 67.   Wing of *Thaumastoptera calceata* Mik.
Text-figure 68.   Wing of *Tonnoiromyia tasmaniensis* Alex.

the radial field. In many respects the group is more generalized than the Limoniaria, despite the great modifications that have taken place in the medial field and the recession of the *m-cu* crossvein. The radial sector is very long, strongly arcuated to feebly angulated at origin, in *O. punctipennis* Alex. (Text-fig. 63) nearly straight, the origin angulated and weakly spurred. The radial field shows a remarkable plasticity of retention and loss of the distal elements. Several species (*O. excessiva* Alex., Text-fig. 62; *O. punctipennis* Alex., Text-fig. 63; *O. andina* Alex.; *D. atribasis* Alex., Text-fig. 66; *D. fumicosta* Alex., Text-fig. 64; *D. flavicosta* Alex.) have retained the distal section of R_1 as a nearly transverse to slightly oblique spur that is sometimes very faint and, when lost, evidently disappears through atrophy. The distal section of R_2 is entirely preserved and very long in *O. excessiva* (Text-fig. 62); *O. pallidibasis* Alex.; *O. alpina* Zett.; *O. dampfi* Alex.; *O. formosicola* Alex.; *D. fumicosta* (Text-fig. 64); still shorter in *O. joana* Alex. (Text-fig. 65); *O. niveitarsis* Alex.; *D. mirabilis* O.S., and others. In some species this tip of R_2 is atrophied but leaves a spur·(*O. punctipennis*, Text-fig. 63). In various species of *Diotrepha*, as *atribasis* (Text-fig. 66) the entire distal section of R_2 is atrophied. The *r-m* crossvein is usually not far from the elements that constitute the cord except in the Australian *O. joana* (Text-fig. 65) where it lies far distad, a condition that is perhaps explained correctly in the original characterization of the species. The radial crossvein, *r*, varies greatly in its extent in the various species (Text-figs. 62-66).

Thaumastopteraria. The subtribe includes only the genus *Thaumastoptera* Mik, with the genotype, *calceata* Mik (Text-fig. 67) and two extinct species from the Lower Oligocene of Northern Europe. The group is obviously close to the Orimargaria but the habits of the immature stages of the two groups are very different and there are certain well-defined correlated structural characters. The radial sector is moderately long, in alignment with R_{2+3} and the long R_3, these three elements forming a gently sinuous curve to the wing-margin; basal section of R_{4+5} strongly arcuated to weakly angulated; R_1 close to the basal section of R_2, *r* being very short; distal section of R_2 entirely atrophied.

Tonnoiromyaria. The subtribe includes only the genus *Tonnoiromyia* Alex. (*tasmaniensis* Alex., Text-fig. 68). The radial sector is long, nearly straight, diverging gently from R_1, in approximate alignment with R_{4+5}; basal section of R_2 lying distad of the level of *r-m*, almost in alignment with R_1, *r* being very reduced and the distal section of R_2 entirely atrophied.

Limoniaria. The various modifications in the present subtribe, which is one of the largest groups of crane-flies, are very complicated and are discussed in some detail in this paper. The primitive condition of the radial field is found in a considerable range of genera, as *Libnotes* Westw., *Peripheroptera* Schin., *Thrypticomyia* Skuse, and others. The condition in *Dicranomyia* (*Thrypticomyia*) *doddi* Alex. (Text-fig. 78) may be discussed as representing this generalized condition, in many respects not being greatly different from the Orimargaria, as described. No member of the subtribe is known to the writer in which the distal section of vein R_2 reaches the wing-margin, as in several Orimargaria, but the extreme tip is atrophied, as shown in the various figures (Text-figs. 70-78). The distal section of R_1 is preserved and lies far before the basal section of R_2, *r* thus being relatively long. The penultimate section of R_1, *r* and the long distal spur of R_2 are all in longitudinal alignment.

The modifications in the subtribe have been brought about in a manner that is illustrated by actual species and may be discussed by means of the following

eight diagrams (Text-fig. 69, 1-8) arranged to show the apparent evolution of the types of venation found in this subtribe.
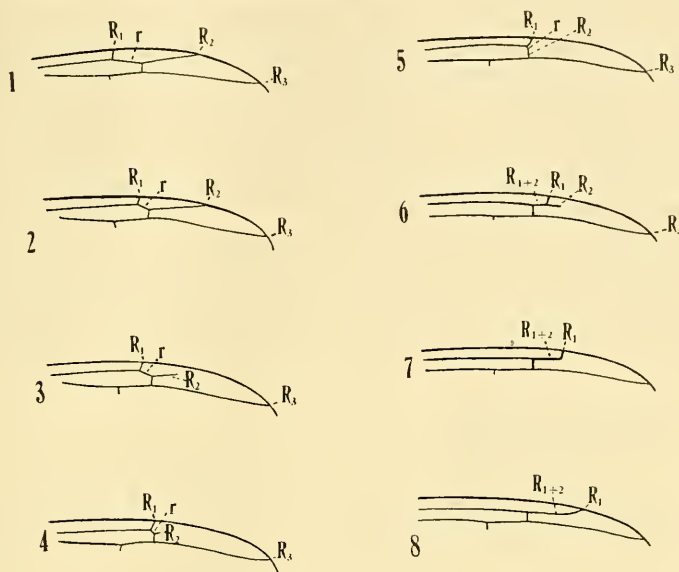

Fig. 69

Text-figure 69. Diagrammatic series to show the evolution of the radial field in the lower Limoniini.

1. The type found in the Orimargaria: R_1 preserved, r elongate, the distal section of R_2 complete, attaining the wing-margin.

2. A further development of Type 1. Note that the free tip of R_1 has moved distad, materially shortening r; distal section of R_2 still entire.

3. Condition as in Type 2 but the tip of R_2 is atrophied back from the margin. Found in many Orimargaria, Limoniaria.

4. An accentuation of Type 3. Note that the atrophy of R_2 is greater and r even more shortened. The result of this is to tend to bring the free tip of R_1 into approximate transverse alignment with the basal section of $R_2 + r$. Found in numerous Limoniaria.

5. A further development of Type 4, where the atrophy of the distal section of R_2 is complete and the free tip of R_1 is in perfect transverse alignment with the combined basal section of $R_2 + r$. This is the commonest type in the Limoniaria, being found in most *Geranomyia* Hal., *Rhipidia* Meig., *Dicranomyia* Steph., some *Limonia* Meig., and others.

6. A type that reverts back to type 3 with a long spur of the distal section of R_2 persisting; the free tip of R_1 has continued its migration distad beyond the level of r and now lies part way out on this spur. Condition found in *Limonia tristigmata* Alex., *Peripheroptera schineri* O.S., and several *Libnotes*, as *greeni*, Edw., *notatinervis* Brun., *regina* Alex., and others.

7. A further modification of type 6 where the free tip of R_1 has migrated to the end of the spur of R_2 but still forms a rectangular bend or even with a tiny spur on R_2 beyond it. In *Libnotes*, as *undulata* Mats.

8. The culmination of the series, where the free tip of R_1 has migrated to the extreme tip of the spur of R_2 and bends to the costa at a gently oblique angle. It should be noted that in this case of the Limoniaria, as in all others here shown beyond type 2, only the free tip of R_1 reaches the costal margin. Found in *Discobola* O.S., a great section of *Limonia*, and other genera.

G

A few of the cases in this largest and most widespread group of crane-flies may be further discussed:

Libnotes Westw. In the genotype, *thwaitesiana* Westw., *r* is very long, meeting the basal section of R_2 in a long gentle curve. In several species of the genus, a condition like type 3 of the diagrammatic series is found (as *L. subaequalis* Alex., Text-fig. 70), being further modified in other species to type 4 (*L. obliqua* Alex., Text-fig. 71). Most of the species fall under type 5. Type 6 is found in *L. greeni, regina* and other species. Type 7 is found in *L. undulata*. Thus in this single genus, we find an unbroken series illustrating five of the diagrammatic types previously discussed.

Limonia Meig. In this genus we find a considerable range in the types, some of which were very puzzling to the writer until the true solution of the venation in this subtribe was finally ascertained. A great many species fall under type 5, with the tip of R_1 and the basal section of R_2 in transverse alignment (as in *parvistigma* Alex., Text-fig. 72; the European *annulus* Meig.; *bifasciata* Fabr.;
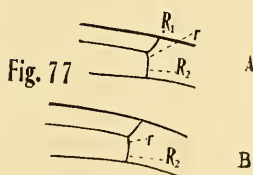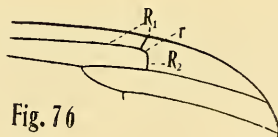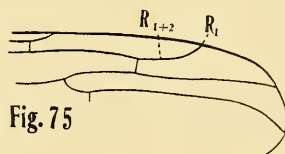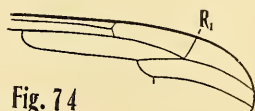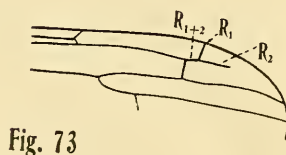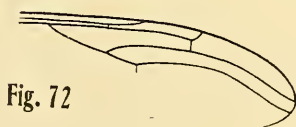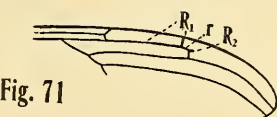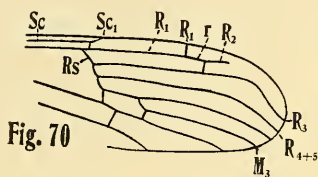
Text-figure 70.   Wing of *Libnotes subaequalis* Alex.
Text-figure 71.   Wing of *L. obliqua* Alex.
Text-figure 72.   Wing of *Limonia parvistigma* Alex.
Text-figure 73.   Wing of *L. tristigmata* Alex.
Text-figure 74.   Wing of *L. fumosa* Alex.
Text-figure 75.   Wing of *Discobola australis* Skuse.
Text-figure 76.   Wing of *Geranomyia picta* Skuse.
Text-figure 77.   A. Wing section of *G. tonnoiri* Alex.; B. Wing section of *G. victoriae* Alex.

quadrinotata Meig.; the Nearctic *californica* O.S.; *cinctipes* Say; *fallax* Johns.; *immatura* O.S.; *solitaria* O.S.; *triocellata* O.S., and others). The other common type in the genus is No. 8, which, at first sight, looks like a long, free distal section of R_2, with the free tip of R_1 atrophied (compare diagrams 1 and 8). There are numerous representatives of this type in the Holarctic fauna (as the European *flavipes* Fabr.; *inusta* Meig.; *nubeculosa* Meig.; *tripunctata* Fabr.; *trivittata* Schumm.; the Japanese *amabilis* Alex.; *amatrix* Alex.; *atridorsum* Alex.; *basispina* Alex., *esakii* Alex. and many others; the Nearctic *indigena* O.S.; *maculicosta* Coq.; *parietina* O.S.; *sciophila* O.S.; *tristigma* O.S., and numerous additional species). In two closely allied New Zealand species, *L. sponsa* Alex. falls between types 4 and 5, while *L. tristigmata* Alex. (Text-fig. 73) has progressed to type 6. In two Neotropical species (*L. fumosa* Alex., Text-fig. 74; *L. insularis* Will.), R_1 bends abruptly down to R_{2+3}, a long, subperpendicular branch that is interpreted as being R_1 thence extending to costa.

Discobola O.S. In the numerous Australian and New Zealand species of this genus (*australis* Skuse, Text-fig. 75) type 8 obtains, the distal serial element being very long and gently arcuated, shortest in *D. tesselata* O.S.

Peripheroptera Schin. The more generalized species (*nitens* Schin.; *eudorae* Alex.) fall in type 3, with *r* long to very long. In other species, *r* becomes more shortened until in some (as *incommoda* O.S.) type 5 is attained.

Dicranomyia Steph. The great majority of the very abundant species fall in type 5, in a few (as *punctipennis* Skuse, *multispina* Alex.; *tarsalba* Alex., and others) with the distal serial element longer than in type 5 but shorter than 8, gently curved to the costal margin. In the subgenus *Idioglochina* Alex., *r* tends to be very elongate, arcuated into the short basal section of R_2. The subgenus
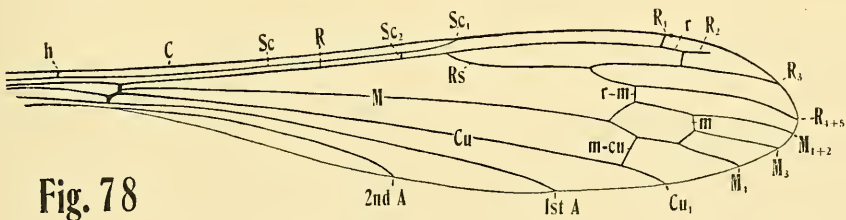

Fig. 78

Text-figure 78. Wing of *Dicranomyia* (*Thrypticomyia*) *doddi* Alex.

Thrypticomyia Skuse (*doddi* Alex., Text-fig. 78) has been discussed under the introduction to the subtribe. In *Euglochina* Alex. the entire radial field beyond the cord is crowded into the wing-tip, occupying the distal fifth or less of the wing; type 5 of the series usually obtains.

Rhipidia Meig. In the numerous species of this genus, type 5 is almost universal.

Geranomyia Hal. The Australian species of this very large genus show a progressive modification from a type shortly beyond 4 (with the spur of the distal section of R_2 atrophied but with a distinct angulation, showing the point of union of *r* and the basal section of R_2; *G. picta* Skuse, Text-fig. 76) to other cases that equal type 5. In *G. tonnoiri* Alex. (Text-fig. 77 A) R_1 is virtually in alignment with the base of R_2 but *r* is still evident as a slight angulated portion near the origin of the distal section of R_1. In *G. victoriae* Alex. (Text-fig. 77 B), *r* and the basal section of R_2 are in perfect alignment, and likewise about in a

transverse line with the distal end of R_1. *G. tridens* Brun. is figured by its author as having the distal section of R_1 retained, being intermediate between types 3 and 5.

Supernumerary crossveins are rather frequently found in this field of the wing; in cell R_3 in the subgenus *Neolimnobia* Alexander (of *Dicranomyia*; type, *diva* Schin.) ; in R_5 in *Dapanoptera* Westw.; in both cells R_3 and R_5 in *Laosa* Edw. and *Libnotes regalis* Edw.

Antocharia. This subtribe includes *Antocha* O.S. and *Orimargula* Mik. In both, Sc and R are closely approximated and the outer portion of R_1 lies close to the strongly incrassated costa. Rs is straight to very gently convex, tending to be
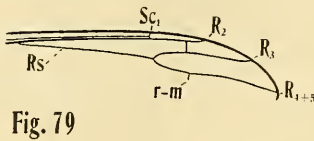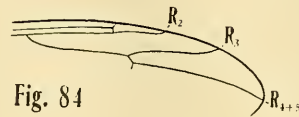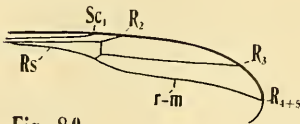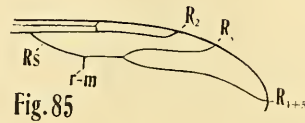

Fig. 79

Fig. 84

Fig. 80

Fig. 85
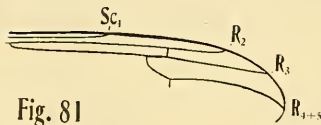
Fig. 81
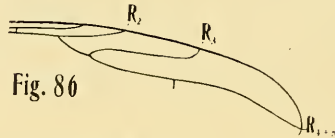
Fig. 86
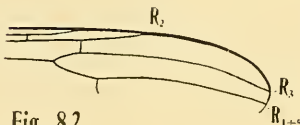
Fig. 82

Fig. 87
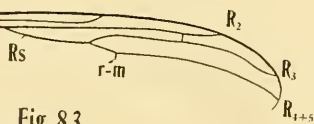
Fig. 88

Fig. 83
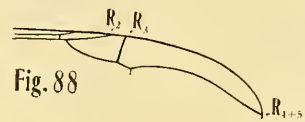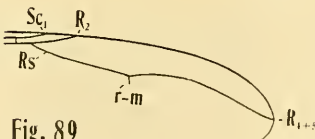
Fig. 89

Text-figure 79.   Wing of *Antocha saxicola* O.S.
Text-figure 80.   Wing of *Orimargula australiensis* Alex.
Text-figure 81.   Wing of *Elliptera tennessa* Alex.
Text-figure 82.   Wing of *Amphilimnobia leucopeza* Alex.
Text-figure 83.   Wing of *Dicranoptycha germana* O.S.
Text-figure 84.   Wing of *Helius venustus* Skuse.
Text-figure 85.   Wing of *Eurhamphidia nivcitarsis* Skuse.
Text-figure 86.   Wing of *Ceratocheilus edwardsi* Alex.
Text-figure 87.   Wing of *C. australasiae* Alex.
Text-figure 88.   Wing of *C. flavirostris* Alex.
Text-figure 89.   Wing of *Toxorhina magna* O.S.

in alignment with R_{4+5}; basal section of R_2 preserved, the distal section very short. In *Orimargula* (*australiensis* Alex., Text-fig. 80), veins Sc_1 and R_2 are more nearly approximated at the wing-margin than in *Antocha* (*saxicola* O.S., Text-fig. 79).

Ellipteraria. The subtribe includes only the genus *Elliptera* Schiner. Rs is elongate, lying very close to and paralleling R_1, in alignment with R_{2+3}; basal section of R_2 preserved in some species (*tennessa* Alex., Text-fig. 81); *jacoti* Alex.; *zipanguensis* Alex.), placed at or shortly beyond the fork of Rs, the section lost by atrophy in other species (*omissa* Egg.; *clausa* O.S.; *astigmatica* Alex., and others); R_3 elongate, in alignment with R_{2+3}; basal deflection of R_{4+5} very strongly arcuated to angulated and spurred (*illini* Alex.) or nearly straight and transverse (*jacoti*).

Amphilimnobiaria. The single genus and species, *Amphilimnobia leucopeza* Alex. (Text-fig. 82) is included. Rs is long, angulated and short-spurred at origin; basal section of R_2 preserved, lying just proximad of the level of *r-m* and opposite the tip of Sc_1.

Dicranoptycharia. The single genus *Dicranoptycha* O.S. (*germana* O.S., Text-fig. 83) is included. Rs is variable in length, the veins at its fork symmetrical; R_{2+3} very elongate, the basal section of R_2 lying far distad, the distal section of R_2 being very short.

Heliaria. Rs is short and often straight. In *Eurhamphidia* Alex. (*niveitarsis* Skuse, Text-fig. 85), *r-m* lies far before the fork of Rs. *Rhampholimnobia* Alex. is similar but *r-m* lies closer to the fork. In *Helius* (*venustus* Skuse, Text-fig. 84), *r-m* is usually on R_{4+5} shortly beyond its origin. In many species of the genus, *r-m* is obliterated by the fusion of vein R_{4+5} on M_{1+2}. In *H. uniformis* Alex., *r-m* is opposite the outer end of cell 1st M_2. In all genera and subgenera of this subtribe, the basal section of R_2 is entirely atrophied.

Toxorhinaria. This subtribe includes the two genera *Ceratocheilus* Wesché and *Toxorhina* Lw. The strict position of the subtribe is still much in doubt and it is placed in the Limoniini with certain misgivings. In the more generalized species of *Ceratocheilus* (*edwardsi* Alex., Text-fig. 86; *australasiae* Alex., Text-fig. 87), the basal section of R_2 appears to have been lost as in the preceding subtribe, the long distal section of R_3 reaching the margin in a gently sinuous curve. In still other species of the genus (*flavirostris* Alex., Text-fig. 88) a progressive shortening of the branch R_3 takes place until it has shortened into a small and nearly transverse element. In *Toxorhina* (*magna* O.S., Text-fig. 89) this vein R_2 is entirely lost but whether by final fusion of the element with R_2 (as previously discussed for the Hexatomine genus *Psaronius* and the Eriopterine genus *Gymnastes*) or by the atrophy of R_3 when it has become short and weak cannot be stated without more evidence.

PHYLOGENETIC CONSIDERATIONS.

The two principal divisions of the Tipulidae have been distinct since at least the middle of the Mesozoic (Upper Liassic), at which time the Architipuline and Tanyderid types co-existed. From the Architipulinae, the Tipulinae (Text-fig. 90) may be derived in almost a direct line. The Cylindrotominae are quite as obviously an offshoot of the Tipulinae. The two Limoniine tribes, Limoniini and Lechriini, that appear to have been evolved from this same general strain have been isolated from the above and from one another for a longer time and it does not seem possible to derive them directly from the Tipuline stem.

The Pediciini have been derived from some pre-existing type that was not conspicuously unlike the recent Tanyderidae. From the Pediciini, through the subtribes Adelphomyaria and Ularia, the tribe Hexatomini is derivable, leading, in turn, through the Hexatomoid Eriopterini to the higher members of the latter tribe. The exact point of origin of the Styringomyiini must be held in question.
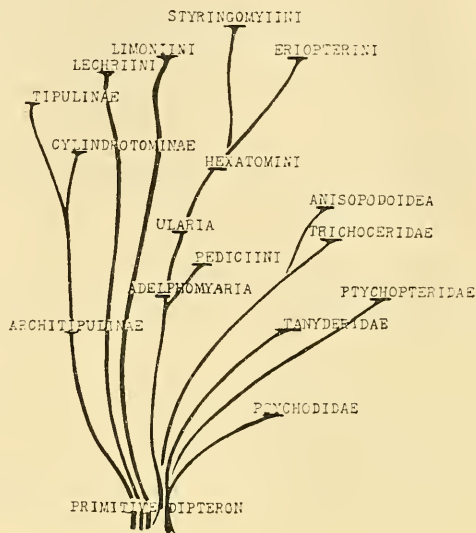
Fig. 90

Text-figure 90.   Phylogenetic Tree.

The Ptychopteridae (*Ptychoptera lenis* O.S., Text-fig. 91) have apparently been derived from the Psychodoid stem, but, if so, they have independently had vein R_2 unite with R_1 to form a short fusion back from the margin, much as in the Pediciini. The Trichoceridae (*Trichocera annulata* Meig., Text-fig. 92), in similar manner, must have been derived from some primitive ancestor in this general region yet it too has undergone the cephalization of vein R_2 and the capture of vein R_4 by R_{2+3}, quite as in the higher Tipulidae. It is highly probable that these

Fig. 91

Fig. 92

Text-figure 91.   Wing of *Ptychoptera lenis* O.S. (Ptychopteridae).
Text-figure 92.   Wing of *Trichocera annulata* Meig. (Trichoceridae).

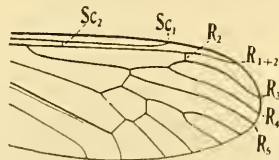two families have led more or less directly to the more specialized groups of Nematocera and thence to the Brachycera, and the correct interpretation of the basal section of R_2 becomes of critical importance in any attempt to trace the phylogeny and correct homologies of the higher Diptera.

Of the other families of Nematocera, the Culicidae, Dixidae, Chironomidae, Orphnephilidae, Anisopodidae, Blepharoceridae, Simuliidae and Bibionidae all agree with the interpretation of the wing, as given, except that the basal section of R_2 in all cases has atrophied and in all except the most generalized forms R_3 and R_4 have fused to the wing-margin. The other Nematocerous groups, with a more highly specialized venation, as the Deuterophlebiidae, Scatopsidae, Sciaridae and Cecidomyiidae offer little direct evidence from the few veins that are still retained in the radial field. From other structures, however, the affinities of the groups with the others above listed render it necessary to interpret the venation as is done in the latter case.

The lower groups of the Orthorrhaphous Brachycera in similar manner agree entirely with the above interpretation, veins R_4 and R_5 remaining distinct as in the Ptychopteridae. From these phylogenetically lower families of Brachycera, the higher groups of the Orthorrhapha and the Cyclorrhapha have been derived.

Summary.

The main points of the preceding discussion may be summarized as follows:

1. The so-called *radial crossvein* (r) in all Diptera except a limited group of the Tipulidae (Tipulinae, Cylindrotominae) is, in reality, the basal section of vein R_2 which has swung cephalad across cell R_1 and fused back from the wing-margin with vein R_1, forming a short or longer fusion, R_{1+2}.

2. There are two distinct lines of specialization in the Tipulidae that have been distinct since at least mid-Mesozoic times. In the *first*, represented by the Limoniine tribes Pediciini, Hexatomini and Eriopterini, the anterior branch of the upper fork of the radial sector (R_2) of the primitive Tanyderoid ancestor has swung cephalad and fused with R_1, as discussed under 1; by a slight shifting of the veins at the end of the sector, the anterior branch of the lower fork of the sector (R_4) becomes more intimately attached to the stem of the upper fork (R_{2+3}) forming a short to longer fusion of veins R_{2+3+4}; in higher groups, veins R_3 and R_4 may become fused to the wing margin, obliterating cell R_3. The basal section of R_2 is present in most cases but in many scattered groups has atrophied, leaving no indication of its previous position. The posterior branch of the sector is thus R_5 alone. In the *second* group, represented by the Architipulinae, Tipulinae, Cylindrotominae, and the Limoniine tribes Lechriini and Limoniini, the true radial crossvein (r) is present but always in a longitudinal or oblique position, forming part of a more or less perfect serial radial vein. In this group, the distal sections of R_1 and R_2 are lost by atrophy. The posterior branch of the sector is interpreted as being a fusion to the margin of veins R_4 and R_5.

3. In some few Pediciini, of the group Dicranotae, there is a supernumerary crossvein in cell R_1 that simulates a true primary crossvein in this cell.

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